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Breeding crops for enhanced micronutrient content

Ross M. Welch[1,3] & Robin D. Graham[2]

[1] *USDA-ARS, U.S. Plant, Soil and Nutrition Laboratory, Tower Road, Ithaca, New York, 14853 USA.* [2] *Department of Plant Science, Waite Campus, University of Adelaide, Glen Osmond, 5064, South Australia.* [3] *Corresponding author**

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Abstract

Micronutrient malnutrition (e.g. Fe, Zn and vitamin A deficiencies) now afflicts over 40% of the world's population and is increasing especially in many developing nations. Green revolution cropping systems may have inadvertently contributed to the growth in micronutrient deficiencies in resource-poor populations. Current interventions to eliminate these deficiencies that rely on supplementation and food fortification programs do not reach all those affected and have not proven to be sustainable. Sustainable solutions can only be developed through agricultural system approaches. One agricultural approach is to enrich major staple food crops (e.g. rice, wheat, maize, beans and cassava) in micronutrients through plant breeding strategies. Available research has demonstrated that micronutrient enrichment traits are available within the genomes of these major staple crops that could allow for substantial increases in Fe, Zn and provitamin A carotenoids without negatively impacting yield. Furthermore, micronutrient-dense seeds can increase crop yields when sowed to micronutrient-poor soils. The enrichment traits appear to be stable across various soil types and climatic environments. Further research is required to determine if increasing levels of micronutrients in staple foods can significantly improve the nutritional status of people suffering from micronutrient deficiencies.

Introduction

While deficiencies of dietary energy (i.e. calories) and protein currently affects more than 800 million people in food insecure regions, incredibly, micronutrient malnutrition (i.e. 'hidden hunger') now afflicts over two billion people, especially resource-poor women, infants and children in the developing world and the numbers are increasing (McGuire, 1993; Yip and Scanlon, 1994). Today, deficiencies of iron, vitamin A and iodine are of most concern to the nutrition community and healthcare officials although other nutrient deficiencies, including zinc, selenium, calcium, magnesium and other vitamins (e.g. riboflavin, vitamin C, vitamin E and folic acid), may be prevalent in some global regions. The consequences of malnutrition create immense economic and societal costs to nations. Micronutrient malnutrition greatly increases mortality and morbidity rates, diminishes congitive abilities of children and lowers their educational attainment, reduces labor productivity, stagnates national development efforts, contributes to continued high population growth rates and reduces the livelihood and quality of life for all those affected (Combs et al., 1996; Combs and Welch, 1998; Welch et al., 1997; Welch and Graham, 1999).

'Hidden hunger' is a capacious, public health issue among nearly all developing nations affecting primarily underprivileged people (Buyckx, 1993; Ramalingaswami, 1995). Disturbingly, the massive increases in the number of people suffering from micronutrient malnutrition over the last four decades (e.g. Fe deficiency anemia has grown from about 30% of the world's population in the 1960s to over 40% during the late 1990s) coincide with the expansion of 'green revolution' production systems. This immense public health problem requires a new paradigm for

* FAX No: 607-255-1132. Tel.: 607-255-5434. E-mail: RMW1@CORNELL.EDU

agriculture; a paradigm that no longer only focuses agricultural research on maximizing food production at minimum expense as the primary goal, but directs some research efforts towards producing enough food crop diversity and nutritional quality of agricultural products to meet human dietary demands. Food systems that feed the world must be changed in ways that will insure that balanced nutrient supplies are available continuously to all people in adequate, affordable amounts (Combs et al., 1996, 1997; Welch et al., 1997).

Past programs to combat micronutrient malnutrition have relied primarily on interventions directed at food fortification or nutrient supplementation programs (Yip, 1997). Unfortunately, these approaches have not proven to be sustainable for various reasons and do not reach all the people at highest risk of developing micronutrient malnutrition. Remarkably, the nutrition community has never embraced agriculture as an important 'tool' to use in fighting 'hidden hunger'. Nor has the agricultural industry viewed agricultural systems as playing an important and explicit role in human nutrition and health. Their efforts have been primarily focused on productivity, efficiency and profit margin issues to drive research and national agricultural programs without regard to either the nutritional quality of the products produced or the adequacy of such systems to meet all the nutritional needs of people (Ross, 1996). Furthermore, institutional and governmental structures and programs have not attempted to link closely agricultural production to human nutrition and health needs, although current knowledge and logic suggest that this should be a high priority for all nations (McGuire, 1993).

Within the agricultural community, plant breeding efforts greatly contributed to advances in staple plant food productivity (mostly cereal crops) during the 'green revolution'. Such breeding efforts, along with improved agriculture technologies, succeeded in providing enough calories and protein to prevent the threatening massive starvation and famines predicted in the early 1960s in many world regions. Importantly, plant breeding can again be used as a powerful weapon to use in fighting 'hidden hunger'. Breeding for micronutrient-enriched staple plant foods is a possibility that should be pursued (Bouis, 1996; Graham et al., 1998, 1999; Graham and Welch, 1996). Success in such a breeding effort would target those groups of people most at risk of developing micronutrient malnutrition because these sectors of societies are dependent on these foods for their sustenance. Furthermore, a plant breeding approach would be sustainable; once micronutrient-dense lines of staple plant foods are developed, there is little additional cost to continue their lineage in ongoing breeding programs for the foreseeable future (Bouis, 1996).

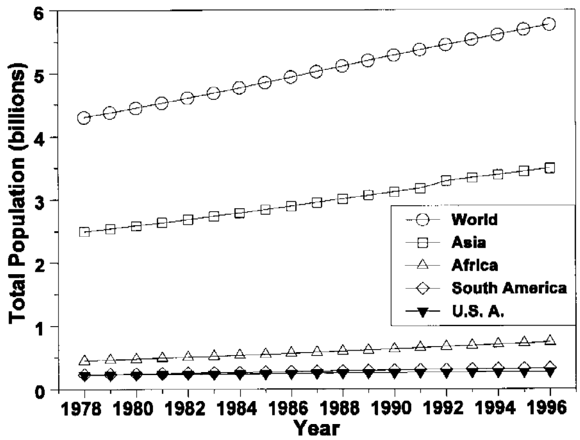

Figure 1. Trends in total population growth in the world, Asia, Africa, South America and the United States between 1978 and 1996 (data from FAO, FAOSTAT Database, 1998).

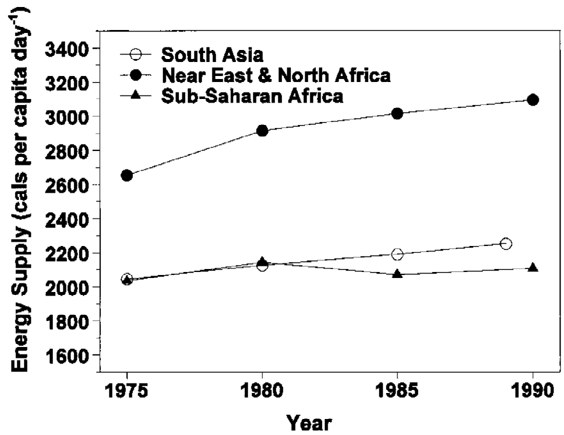

Figure 2. Trends in dietary Energy Supplies from 1975 to 1990 in some world regions (data from UNACCSN, 1992).

Reasons for concern

The extraordinary success of agricultural research during the last five decades provided many developing countries with the tools necessary to increase dramatically cereal production and feed a rapidly growing population (see Figure 1). For example, in the Near East/North Africa, in Sub-Saharan Africa and in South Asia food supply (in terms of dietary energy supply per capita per day) has kept up with population growth

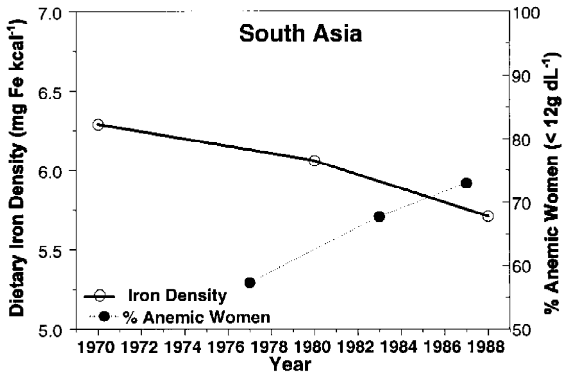

Figure 3. South Asian trends in dietary Fe density and in Fe deficiency anemia in women from 1970 to 1988 (data from FAO, 1990; UNACCSN, 1992).

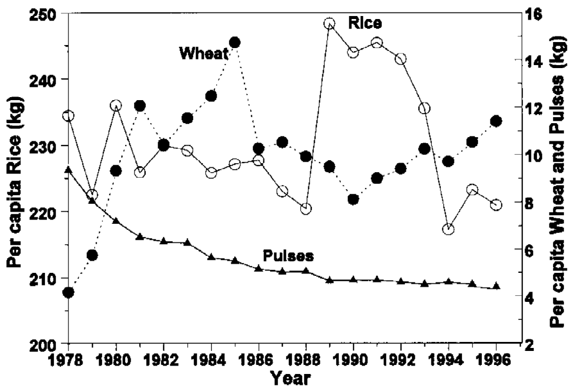

Figure 4. Per capita trends in total rice, wheat and pulses production in Bangladesh from 1978 to 1996 (data from FAO, FAOSTAT database, 1998).

(see Figure 2). However, only just producing enough calories (i.e. energy) has resulted in unforseen nutritional problems for nearly 50% of the world's people, especially among the poor (UNACCSN, 1992).

'Green revolution' cropping systems may have contributed to some unforeseen negative consequences on human nutrition and health. For example, in South Asia, the introduction of high input, modern wheat/rice cropping systems are associated with time trends in the growth of Fe deficiency anemia among poor pre-menopausal women, and negatively correlated to dietary Fe density (mg Fe kcal^{-1} of available food; Figure 3). Data from China, Sub-Saharan Africa, South America, Middle America/Caribbean and Southeast Asia also show the same trends (UNACCSN, 1992).

What are the causal factors responsible for the incredible growth in 'hidden hunger' worldwide? Has agriculture unintendedly contributed to the growth in micronutrient malnutrition? Answers to these questions are not clear. However, changes in cropping systems may have contributed significantly to the growth in 'hidden hunger'. Clearly, the use of modern cereal cropping systems in many developing nations has been paralleled by a decreased per capita production of traditional edible legume crops which contain much higher levels of most micronutrients (Welch et al., 1997). This has resulted in lower availability and higher prices of many micronutrient-rich pulses at least in some world regions (Anonymous, 1993, 1994; Combs et al., 1996; Uvin, 1994; WHO, 1996; Yip, 1997). For instance, on the one hand, from 1978 and 1996, per capita rice and wheat production in Bangladesh kept pace with or exceeded population growth, while on the other, total pulse production dramatically decreased during this time frame (Figure 4). Interestingly, data complied by the Food and Agricultural Organization, United Nations (FAO), show negative trends in Fe density in South Asian diets (FAO, 1990) and an increase in Fe deficiency anemia among women (UNACCSN, 1992; WHO, 1996) during the development of green revolution cropping systems. Possibly, those changes in agricultural systems that occurred in South Asia during the green revolution resulted in dramatic increases in rice and wheat production, but at the expense of pulse production, iron density in the diet and women's Fe status. Possibly, losses in the availability of pulses for human consumption may be an important contributing factor to the rise in 'hidden hunger' in South Asia because edible legume seeds are a much richer source of micronutrients than cereals, especially after the cereal grains have been milled and/or polished before consumption (Welch et al., 1997).

Current data collected on the extent of micronutrient malnutrition in humans on earth only cover Fe, I and/or vitamin A deficiencies (Mason and Garcia, 1993; Ramalingaswami, 1995; UNACCSN, 1992; Uvin, 1994). Most certainly, several other micronutrients, including Zn, Cu, Se and other vitamins (e.g. riboflavin, vitamin C and vitamin B_{12}), are limiting in the diets of large numbers of people in many regions of the world (although little is known about the actual extent of these deficiencies because of technical and clinical problems in determining their numbers and distribution globally) (WHO, 1996).

The world nutrition community has made combating 'hidden hunger' a high priority (Anonymous, 1992, 1995, 1996). Interestingly, certain micronutrient deficiencies (especially Fe deficiency) are an issue even in developed countries such as the United States and Canada (Frazao, 1996; Welch et al., 1997).

Consequences of 'hidden hunger' to human health and felicity

Health consequences

Micronutrient malnutrition diminishes the motivation and curiosity of infants and young children, thereby reducing their exploratory activities including their development (Grantham-McGregor and Ani, 1999; Mongeau and Larivee, 2000). Consequently, this ailment impairs mental and cognitive abilities by reducing interactions of children with their environment, their peers and their family. These children, deprived of their full genetic potential for mental and physical development, become adults with lower intellectual and physical abilities. They are less able to provide for themselves and their families. Often they are less productive with higher rates of chronic disease and associated disabilities. National economic losses to some countries resulting from 'hidden hunger' can be as high as 5% of their gross national product in lost lives, disabilities, healthcare costs and labor productivity. In Bangladesh and in India, a total of $18 billion was calculated to be lost from their economies each year as a result of micronutrient malnutrition (Islam and Tori, 1998).

Rapid growth during fetal development, infancy, childhood and adolescents demand greater intakes of micronutrients. Growth failure or deficiency diseases will develop without increased intakes. Micronutrient deficiency symptoms are most prevalent during these stages of life. Also, interactions between micronutrient deficiencies and infectious diseases are very important. These interactions can confound healthcare efforts to control various diseases (such as the synergistic interaction between vitamin A deficiency and measles; increased severity of measles leading to vitamin A-deficiency-blindness and death). Malaria and hookworm infections are also associated with Fe deficiency anemia. Not withstanding the difficulties in associating micronutrient deficiencies directly to many diseases, clearly, prevention of these deficiencies can contribute to infectious disease control (Ramalingaswami, 1995).

A high risk of tissue hypoxia and heart failure, which can lead to death in young children and pregnant women, is associated with Fe deficiency (Viteri, 1998). Maternal anemia, aggravated by blood loss during child birth, is reported to be responsible for most of the maternal mortality during birth in the world (20% of all maternal deaths are attributed to Fe deficiency anemia (Maberly et al., 1994) and 30% of all children who enter hospitals with severe anemia die (Anonymous, 1994). Babies born to mothers that are iron-deficient are commonly stunted and unhealthy. Children suffering from Fe deficiency have poor attention spans, impaired fine motor skills and less capacity for memory (Walter et al., 1997). Iron deficiency in pregnant women may cause irreversible damage to fetal brain development leading to irreversible damage to intellectual development in their babies (Gordon, 1997). Iron deficiency in pregnant women is correlated to infant prematurity and low birth weight; this can result in long-term frailties such as immune system dysfunctions and growth failure (McGuire, 1993). Iron deficiency reduces both physical performance and work productivity. For example, plantation workers in Indonesia, cotton mill workers in China and workers in Sri Lanka when provided Fe supplements increased their productive work output by 20–50% (Anonymous, 1994; Li et al., 1994; Maberly et al., 1994). Some economic studies suggest that the calculated benefit/cost ratio from giving iron supplements to anemic workers is potentially as high as 260:1. In Fe fortification studies, the value of benefits, in terms of labor output, from fortification was reported to be 7, 42 and 70 times the cost of the fortification programs in field trials in Indonesia, Kenya and Mexico, respectively (Sanghvi, 1996).

Iron, vitamin A and I deficiencies are associated with increased mortality rates among resource-poor women, infants and children (McGuire, 1993). Additionally, Vitamin A deficiency is the most important cause of childhood blindness in developing nations. Vitamin A deficiency impairs the integrity of epithelial tissue barriers (e.g. skin) to infection. The immune system is also affected leading to increased severity of certain infections and increased risk of childhood death.

High rates (about 0.5–1%) of neonatal deaths and still births are associated with maternal I deficiency. Additionally, severe I deficiency in pregnant women results in irreversible mental retardation and neurological disorders (cretinism) in their babies. Other I deficiency disorders (IDD) include deafness, muteness and mild to moderate mental retardation. All of these outcomes are all irreversible. They limit children's ability to learn, their educational attainment, their occupational choices and ultimately, their future livelihoods and welfare. In nations with prevalent IDDs, there is an immense cost to societies in terms of lost human potential and its economic ramifications (WHO, 1996).

Acute Zn deficiency in humans is relatively rare resulting in hypogonadism and dwarfism in men, growth retardation in infants and children, orificial and acral dermatitis, diarrhea, alopecia, impaired reproductive performance and difficulty in parturition (Gibson, 1994; Prasad, 1993, 1996; WHO, 1996). Importantly, marginal Zn deficiency may be wide spread, but unreported globally because there is no established clinical method for determining marginal Zn deficiency in humans (Endre et al., 1990; Larsen, 1997; Reinhold, 1988; Shrimpton, 1993). Mild Zn deficiency reduces growth rates in infants and children, impairs resistance to infection, reduces taste acuity, increases the severity and duration of diarrhea and delays wound healing (WHO, 1996). Additionally, evidence is accumulating that mild Zn deficiency also impairs brain function and behavior in children (Penland, 1997). Furthermore, several reports suggest that Zn is an antioxidant involved in antioxidant defense systems, but the exact mechanism is not known. Kim et al. (1998) showed that marginal zinc deficiency lowers the lymphatic absorption of vitamin E (α-tocopherol) in rats. Thus, intestinal absorption of vitamin E is reduced by low-Zn status. Therefore, Zn status may have a profound effect on the bioavailability of lipid soluble vitamins like vitamin E.

Much attention has recently focused on the interaction between I and Se because of Se's role in thyroid hormone metabolism (as a constituent of iodothyronine $5'$-deiodinase). Combined deficiencies of Se and I may have adverse effects on infant growth, development and survival. Selenium deficiency could also be a problem in areas where I deficiency disorders are not clearly related to I intakes and where the diet is also low in available Se (Hofbauer et al., 1997; WHO, 1996).

Societal and development consequences

Linear conceptualizing can lead to the conclusion that improving the nutritional health of people will result in increased population growth rates. History, however, suggests that this is not true. In countries that have dramatically reduced the incidence of malnutrition have concurrently reduced their birth rates dramatically over the last century (such as Japan and other industrialized countries). Evidence is accumulating showing that improved nutritional health promotes reductions in the birth rate (Behrman, 1993; Sanghvi, 1996). This should be especially true for micronutrients that are known to play critical roles in fetal brain development and in congnitive ability during infancy and childhood (e.g. Fe, I, Zn, B). Unchecked micronutrient malnutrition in a society will lead to more unhealthy people, reduced labor productivity, lower educational attainments in children, reduced school enrollments and attendance, earlier marriages, increased morbidity and mortality, lower standards of living, higher health care costs and civil discontent. This may lead to governmental instability and political unrest. Adequate nutrition for pregnant women, infants and children will lead to better school attendance, higher educational attainment, and ultimately, higher family incomes, later marriages and improved worker productivity – all outcomes that enhance civilization and lower birth rates. Eliminating 'hidden hunger' should be a high priority for all nations.

Breeding for micronutrient-dense crops

Physiological bases of micronutrient accumulation

The physiological basis for micronutrient efficiency in crop plants and the processes controlling the accumulation of micronutrients in seeds is not understood with any certainty. Because of space limitations and the complexity and volume of literature available, these subjects will not be covered in this short review. For an in-depth discussion of these topics, the reader is referred to the following references (Graham and Welch, 1996; Marschner, 1995; Welch, 1995, 1999; Yang and Römheld, 1999). A brief outline of these processes that determine micronutrient concentrations in edible plant tissues follows.

There are several barriers to overcome in genetically modifying plants to accumulate more micronutrient metals (e.g. Fe and Zn) in their edible parts. These barriers to micronutrient uptake and distribution in plants are the result of tightly controlled homeostatic mechanisms that regulate micronutrient uptake and distribution in plants assuring adequate, but nontoxic levels of these nutrients to accumulate in plant tissues. The first and most important barrier to micronutrient uptake reside at the root-soil interface. To increase micronutrient metal uptake by roots, the available levels of the micronutrient in the rhizosphere must be increased to allow for more absorption by root cells. This could be enhanced by stimulating certain root-cell processes that modify micronutrient solubility and movement to root surfaces (Welch, 1995), such as by stimulating root-cell H^+, metal chelating compounds and reductants release rates, and increasing root absorptive surface area such as number and extent of fine roots and root hairs. Second, the root-cell plasma membrane absorption mechanisms (e.g. transporters and ion channels) must be sufficient and specific enough to allow for the accumulation of micronutrient metals once they enter the apoplasm of root cells from the rhizosphere. Third, once taken up by root cells, the micronutrients must be efficiently translocated to edible plant organs. For seeds and grains, phloem sap loading, movement and unloading rates are important characteristics to consider in increasing micronutrient metal accumulation in seeds and grains.

The international breeding effort

The current thrust of research is to determine the genetic potential for increasing the concentrations of bioavailable Fe, Zn and provitamin A carotenoids (as well as Se and I) in edible portions of several staple food crops including rice, wheat, maize, beans and cassava (Bouis, 1996; Graham et al., 1998, 1999; Graham and Welch, 1996). The following discussion reviews the findings to date that have been obtained in this on-going effort.

Breeding criteria for improving micronutrient density

Certain conditions must be met before new lines of micronutrient-rich staple food crops are distributed globally to national agricultural research programs. Meeting these conditions will assure that targeted people at risk of developing micronutrient malnutrition will benefit from such action. These conditions are listed below.

1. Crop productivity (i.e. yield) must be maintained or increased to guarantee widespread farmer acceptance.
2. The micronutrient enrichment levels achieved must have significant impact on human health.
3. The micronutrient enrichment traits must be relatively stable across various edaphic environments and climatic conditions.
4. Ultimately, the bioavailability[1] of micronutrients in enriched lines must be tested in humans to assure that they are of benefit to people preparing and eating them in traditional ways within normal household environments.
5. Consumer acceptance must be tested (taste and cooking quality must be acceptable to household members) to assure maximum impact on nutritional health.

Meeting these conditions will require a new way of thinking and performing research by most agriculturalists including plant breeders, a holistic food systems view of agricultural production. It will necessitate that researchers co-operate with various specialists in disciplines not normally associated with agricultural research, including nutritionists, public health officials, sociologists and economists, to assure that their efforts will have meaningful impact on human nutrition and health (Combs et al., 1996).

The question of yields

The effects of breeding for micronutrient-dense staple seeds and grains on crop yields have been addressed in a number of recent reviews (Bouis, 1996; Graham et al., 1998, 1999; Graham and Welch, 1996). Briefly, increasing the micronutrient stores in seeds results in more seedling vigor and viability enhancing the performance of seedlings when the seeds are planted in micronutrient-poor soils. This improved seed vigor allows for the production of more and longer roots under deficient conditions allowing seedlings to scavenge more soil volume for micronutrients and water early in growth, an advantage that can lead to improved yields compared to seeds with low micronutrient stores when grown under micronutrient stress conditions. Many of the countries where micronutrient deficiencies in humans are a problem are also countries that have large areas of micronutrient-poor/deficient soils (White and Zasoski, 1999). Thus, improving seed vigor with respect to micronutrient stores should be very beneficial to agricultural production in these countries. Additionally, disease resistance and stress tolerance are improved in micronutrient-dense seeds which would also aid agricultural production in target countries (Welch, 1986, 1999). Thus, selecting for these traits in staple food crops is a ‘win-win’ opportunity. It has potential to enhance crop yields without additional

[1] Bioavailability is defined as that amount of a nutrient in a food-constituent of a meal that is absorbable and utilizable by a person eating the meal.

farmer inputs and to improve their nutritional quality at the same time.

The genetic potential

Over the past several years, scientists have collecting data on the potential for breeding for significant levels of bioavailable Fe, Zn and provitamin A carotenoids in rice, wheat, maize, beans and cassava. The discussion below summarizes the findings to date.

Bean

Researchers at the *Centro Internacional de Agricultura Tropical* (International Center for Tropical Agriculture; CIAT) have been studying the degree of genetic variability that exists in Fe and Zn concentrations in seeds of common beans (*Phaseolus vulgaris* L.) (Graham et al., 1999). Beebe (pers. comm.) evaluated a core collection of over 1000 accessions of common beans and found a range in Fe concentrations from 34 to 89 μg g^{-1} Fe (average = 55 μg g^{-1} Fe). Zinc concentrations in these same accessions ranged from 21 to 54 μg g^{-1} Zn (average = 35 μg g^{-1} Zn). Some bean accessions from Peru were recently found to contain especially high levels of Fe averaging over 100 μg g^{-1} Fe. The range in seed-Zn concentrations in the core collection was narrower than seed-Fe concentrations ranging from 21 to 54 μg g^{-1} Zn. Wild types tended to have lower Zn concentrations than common cultivated types. Some seeds from genotypes originating in Guatemala were highest in Zn levels. The data collected suggest that there is sufficient genetic variability to increase significantly Fe (by about 80%) and Zn (by about 50%) concentrations in common beans. Results also indicate that the traits responsible for genetic improvements in Fe and Zn concentrations are stable across various environments. For both Fe and Zn seed concentrations, there were significant location and location $\times$ genotype effects demonstrating (as expected) that environments can influence the concentrations of Fe and Zn in bean seeds. However, high-Fe and high-Zn genotypes will accumulate more of these nutrients when compared to low-Fe and low-Zn genotypes grown at the same location during the same growing season.

Interestingly, CIAT researchers also found a very highly significant positive correlation of 0.52 between the concentrations of Fe and Zn across different genotypes. Thus, genetic factors for increasing Fe are co-segregating with genetic factors increasing Zn. Therefore, selecting for higher Fe level in bean seeds will also select for increased Zn levels in the seeds.

Table 1. The mean and range in concentrations (dry weight basis) of Fe and Zn in six sets of brown rice germplasm (939 genotypes) grown under similar conditions at IRRI, Los Bãnos, Philippines (Table modified form Graham et al., 1999)

Genetic sets	Fe (μg g^{-1})		Zn (μg g^{-1})	
	Mean ±SE[a]	Range	Mean ±SE	Range
Traditional & improved lines	13±2.6	9.1–22.6	24.0±4.7	13.5–41.6
IRRI breeding lines	10.7±1.6	7.5–16.8	25.0±7.6	15.9–58.4
Traditional & improved lines	12.9±3.1	7.8–24.4	24.4±4.7	16.5–37.7
Tropical japonicas	12.9±1.5	8.7–16.5	26.3±3.8	17.1–40.1
Popular lines & donors	13.0±2.5	7.7–19.2	25.7±4.6	15.3–37.3
Traditional & improved lines	13.8±2.3	10.8–18.0	24.2±4.1	19.9–33.3

[a] ±SE = ± standard error of the mean.

Rice

Since 1992, researchers at IRRI have been evaluating the genetic variability of Fe concentration in rice grain. In 1995, the research was expanded to include Zn (Graham et al., 1999). Table 1 shows the results obtained for some of this research. The range in Fe and Zn concentrations within the six sets of genotypes (n=939) tested in this study were 7.5 μg g^{-1}–24.4 μg g^{-1} for Fe, and 13.5 μg g^{-1}–58.4 μg g^{-1} for Zn. Thus, within those genotypes tested, there was about a four-fold difference in Fe and Zn concentrations suggesting some genetic potential to increase the concentrations of these micronutrients in rice grain.

Among the highest grain-Fe concentrations (i.e. ranging from about 18 μg g^{-1} to 22 μg g^{-1}) found were in a number of aromatic rice varieties including Jalmagna, Zuchem and Xua Bue Nuo. Additionally, these same aromatic lines also contained the highest grain-Zn concentrations (ranging from about 24 μg g^{-1} to 35 μg g^{-1}). Further research using F2-derived populations demonstrated that the aromatic trait was not pleiotropic for grain-Fe or grain-Zn concentrations and, therefore, this trait may be used to screen for high Fe and Zn levels in rice grain but the linkage is broken at a low frequency.

Several studies were carried out at IRRI to examine the effect of soil and climatic factors on grain-Fe and grain-Zn concentrations among genotypes. Factors studied included wet season-dry season, normal-saline soils, acid- neutral soils and N-supply. The data from these various studies demonstrated that high-Fe and high-Zn grain traits are expressed in all rice environments tested although there is some evidence of significant genotype × environment interactions that can ultimately affect Fe and Zn concentrations (Graham et al., 1999) in extreme environments.

These IRRI results indicate that there is significant genetic diversity in the rice genome to increase substantially Fe and Zn concentrations in rice grain. However, the effects of rice grain processing on Fe and Zn levels in the edible product (i.e. polished and parboiled rice grain), as well as the bioavailability of the Fe and Zn in the grain to humans still await final results from continuing evaluations of these factors.

Wheat

A wide range of wheat germplasm is being studied at CIMMYT with respect to the concentration of Fe and Zn in the whole grain and environmental interactions on their concentrations. In one study, the ranges in Fe and Zn concentrations (dry weight basis) in wheat grain from plants grown in El Batan, Mexico in 1994 were 28.8–56.5 μg g^{-1} (mean = 37.2 μg g^{-1}; S.D. = 4.10 μg g^{-1}; n=132) for Fe and 25.2–53.3 μg g^{-1} for Zn (mean = 35.0 μg g^{-1}; S.D. = 4.99 μg g^{-1}; n=132) (Graham et al., 1999). Clearly, enough genetic variation exits within the wheat germplasm to substantially increase Fe and Zn concentrations in wheat grain. Among all wheat germplasm studied, species *Triticum dicoccum* Schrank had the highest concentrations of Fe and Zn, which warrants further study.

There was a high correlation between grain-Fe and grain-Zn concentrations in the wheat lines studied. While there was significant genotype × environmental interactions obtained for Fe and Zn grain concentrations, there was still a strong genetic component to Fe and Zn accumulation in the grain. This finding indicates that it should be possible to improve Fe and Zn levels in wheat grain simultaneously through plant breeding. Additional research has also shown that there is no negative linkage between grain yield and Fe and Zn density in the grain.

Maize

Current data being collected by CIMMYT suggests that the range in Fe and Zn concentrations in maize kernels is not as great as that found for other cereal crops, although more data are needed to confirm this finding (M. Banziger, pers. comm. CIMMYT). A Southern African germplasm collection containing 20 lines was evaluated at Harare, Zimbabwe in 1996–97. The range in Fe and Zn concentrations was 16.4–22.9 μg g^{-1} for Fe (mean of 19.6 μg g^{-1}), and 14.7–24.0 μg g^{-1} for Zn (mean of 19.8 μg g^{-1}). In earlier studies, CIMMYT reported a much wider range in Fe and Zn concentrations during evaluations of 1486 germplasm from 1995 to 1998 that included a wide range of landraces, varieties and breeding germplasm from CIMMYT and 57 germplasm from Southern Africa. In the earlier trials, genotypes high in grain-Fe and grain-Zn concentrations exceeded trial means by as much as 50%. For example, in an evaluation of 1045 breeding lines from Zimbabwe during the 1995/96 growing season, the range in Fe concentrations was from 17.7 to 61.8 μg g^{-1}. Zn concentrations in these same lines varied from 12.9 to 28.5 μg g^{-1}. The discrepancy between the earlier and later data sets may be the result of Fe and Zn contamination of the maize kernels analyzed, but further research is needed to verify this possibility.

Cassava

The variation in β-carotene concentration in cassava roots from a CIAT core collection (630 genotypes) from the global cassava germplasm collection (about 5500 genotypes) was reported by Iglesias et al. (1997). Additionally, the relationship between root color and heritability as well as the stability of root-β-carotene to different root-processing techniques was studied. They reported a range in β-carotene concentrations in fresh roots from 0.1 to 2.4 mg 100^{-1} g.

The inheritance of β-carotene root-concentration appears to be determined by two genes (one controlling transport of shoot precursors to roots and one responsible for the biochemical processes affecting the accumulation of β-carotene in the root). Furthermore, visual screening by using intensity of orange color seemed feasible. However, they also stated that there was a need to rely on quantitative screening techniques to increase the efficiency of the screening program. It is possible that other provitamin A carotenoids could also be responsible for the deep yellow colour observed in accessions that have intermediate β-carotene concentrations.

Iglesias et al. (1997) concluded that there is enough genetic variability within the available cassava germplasm that would make it possible to produce cassava-roots that contain enough β-carotene to meet the daily requirements of adults (i.e. 6 mg d^{-1} β-carotene) if the β-carotene in cassava roots is bioavailable. The genotypes containing the highest levels of β-carotene were collected from the Amazonian region of Brazil and Colombia where yellow-root lines are preferred by the indigenous farmers. Processing techniques were shown to have a large effect on the final β-carotene content in the food prepared from cassava roots with some genotypes being more stable to various forms of processing then others. This factor must also be included in any breeding program to increase β-carotene in cassava roots.

Summary

There is very compelling global human health and nutritional evidence to persuade plant breeders to include micronutrient density traits as primary objectives in their work targeted to the developing world (see also extended discussions of this issue in Combs et al., 1996; Welch et al., 1997; Welch and Graham, 1999). Furthermore, doing so should also improve crop productivity when micronutrient-enriched seeds and grains are planted to micronutrient-poor soils (Graham and Welch, 1996). Current evidence suggests that there is enough genetic diversity within the genomes of staple plant foods to accomplish this task. Succeeding in doing this would dramatically contribute to improving the health, livelihood and felicity of numerous resource-poor, micronutrient-deficient people in many developing countries, and would contribute greatly to sustaining national development efforts in these countries, and at the same time, should help to lower the birth rates in these countries. Without such a breeding effort, finding sustainable solutions to micronutrient malnutrition will not be forthcoming in the foreseeable future.

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